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THE MORPHOLOGY, DEVELOPMENT AND ECONOMIC ASPECTS OF SCHIZOPHYLLUM COMMUNE FRIES

BY

FREDERICK MONROE ESSIG

A THESIS ACCEPTED IN PARTIAL SATISFACTION OF
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A Thesis in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy in the
University of California Presented in
Nineteen Hundred and Twenty by

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I. INTRODUCTION

The peculiar split character of the gills of *Schizophyllum* called the attention of botanists to this genus in comparatively early times. Mention of this fungus appeared in Dillenius' "Catalogus plantarum sponte circa Gissam nascentium" more than 200 years ago. Since that time (1719) it has been frequently collected and described, and in the last quarter-century has been reported to be of considerable economic importance, but the literature upon the common *Schizophyllum* is singularly fragmentary and incomplete. Early mention was in the form of collection notes or brief descriptions of the dried sporophores. Many of these appeared in print between the time of Dillenius and the latter part of the 19th century.

In 1884 W. G. Smith found *Schizophyllum* growing upon ensilage. This is the earliest mention of its economic importance in available literature. Since this article appeared *Schizophyllum* has been reported as parasitic upon a large variety of hosts, but papers relating to the exact nature of the parasitism are not to be found.

There is also very little published concerning the microscopic structure of the sporophores or vegetative hyphae. A few sentences and one figure in Buller's "Researches on Fungi" (1909) give an inkling as to the structure of the hymenium and hyphae composing the gills. No mention or illustration of contained protoplasmic structure has been found. Rumbold (1910) described and featured the walls of the vegetative hyphae, but did not mention the cell contents.

The literature upon the morphology of the sporophores, however, is much more complete than that upon the microscopic structure. Early descriptions were mostly confined to the structure of desiccated specimens. Hasselbring in 1907 called attention to the development of the sporophores and the peculiar relationship of the hymenophore to the pileus and stipe. Buller (1909) gave a full description of the mature sporophores, origin of the secondary lamellae, marginal splitting, and incurving of the lamellar plates. Adams (1918) described the origin and development of the lamellae. The phenomena he describes, however, do not agree with the phenomena displayed by sporophores growing in their normal habitat on the University of California campus.

This paper is presented in an effort to give a more accurate and complete description of the sporophores; a description of the microscopic structure of the hyphae which go to make up the sporophores and the vegetative mycelium; an account of the origin and development of the gills as found in specimens growing in the field at Berkeley, California; and a report on the economic aspects of the fungus.

According to Saccardo (1887–1895), there are twelve species of *Schizophyllum,* all of them being tropical or subtropical except *S. commune* Fries, which is distributed throughout the northern and southern temperate zones. Hennings (1898) stated that all of the twelve forms described probably constituted only two or three distinct species, and this view seems to the writer to be more nearly correct. The original work reported in this paper is confined entirely to *Schizophyllum commune* Fries,[1] but in the table of geographical distribution and the list of host plants reference is made to the genus as a whole, as it is extremely difficult to distinguish between the one species of the temperate zones and the several tropical species described.

II. MATERIAL AND TECHNIQUE

The sporophores studied came from three sources:

1. Decayed wood in the field.
2. Decayed wood kept in moist chambers in the laboratory.
3. Specimens from the Herbarium of the University of California.

The specimens obtained from the field were collected over a period extending from September, 1917, to February, 1920. They were found growing under natural conditions upon the wood or bark of *Acacia* sp., *Quercus agrifolia,* and *Umbellularia californica.* In all several hundred specimens have been collected, ranging in age from apparently a few hours to two years, and in size from less than 1 mm. to 5 or 6 cm. in diameter. More than a hundred specimens of very young sporophores were obtained during the autumn of 1919 from a single log of *Umbellularia* partly imbedded in gravel along a small creek near the laboratory.

As an experiment short sections of small trunks and branches of trees infected with *Schizophyllum* were placed in shallow pans of water and covered with bell jars. Air was admitted by supporting the bell

[1] For a complete list of synonyms see Greville (1824) and Murrill (1915). The most important are *Agaricus alneus* Linnaeus, *Schizophyllum alneum* Schroeter, *Schizophyllus alneus* Murrill.

jars so that the lower edge did not quite touch the surface of the water. Under these conditions sporophores could be induced to grow throughout the year, new ones appearing successively as the mature specimens were removed. In this way the development of the sporophores could be watched from day to day and compared with conditions found in the field. It might be stated here that at no time was there any essential difference between specimens found in the field and those grown in moist chambers in the laboratory. The moist chambers also furnished an excellent opportunity for the study of regeneration phenomena.

In the third source of material, the Herbarium of the University of California, specimens from many localities in California are preserved, as well as some from Whidbey Island, Washington; from Ontario, Canada; and from France. These sporophores were used for comparison with respect to general morphological characters.

In the matter of technique no claim is made for originality. It was found at the beginning of the work that the processes used in the treatment of the fleshy fungi did not give satisfactory results when applied to *Schizophyllum*. After experimenting with many methods those outlined below were found to be the best suited for use with this fungus.

The killing and fixing agent used for the young sporophores was a 70 per cent solution of alcohol with 6 c.c. of commercial formalin added to each 100 c.c. of the alcoholic solution. This not only killed and fixed the material but preserved it indefinitely. Spores were caught in a film of albumen fixative on a slide and fixed in 100 per cent alcohol, thus hardening the fixative and fastening the spores to the slide.

Most of the sectioning was done on a rotary microtome, the material being frozen in a solution of gum arabic (compare Gardner, 1917). Some of the specimens were imbedded and sectioned in paraffin, but this method did not give good results, as the material became hard and difficult to section. The sporophores for the study of early developmental stages were sectioned individually, and all the sections from a single specimen were preserved in a vial. From these vials the sections were poured into shallow dishes where all could be seen. Only those sections cut at or near the median plane were selected for mounting. Albumen fixative was used to fasten the sections on the slide. Great care was used in orienting the imbedded sporophores before sectioning, as oblique sections through the revolute hymenial margins

lead to entirely erroneous interpretations of the structure of the sporophore. Thus sections cut obliquely through specimens with well developed "gills" which can be seen unmistakably with the unaided eye appear as though the hymenium lined a series of chambers, or as if the "gills" in the middle of the section were normal, with "hymenial chambers" at each edge. Certain sections cut in this manner corresponded in many ways to figures given by Adams (1918). Material for young developmental stages was sectioned from 20 to 25μ in thickness so that the sections would remain entire. For cytological work the sections were cut 5 and 10 micra thick. Sections as thin as 5 micra will not hold together well, so that, for the finer structure, it was necessary to use only fragments.

Flemming's triple stain was used for some sections, but was not so satisfactory as safranin alone. Using a two-minute period in a 3 per cent solution of safranin in 50 per cent alcohol and washing out rapidly, a fair differentiation was obtained. The nuclei stain deep red, the cytoplasm a very light pink, and the cell walls an intermediate shade. All efforts to make the nuclei stand out more clearly by counterstaining resulted in failure. For staining spores, a 48-hour period was needed, as in a shorter period the stain would be almost entirely removed in the washing-out and dehydrating operations preceding clearing and mounting. The sections and spores were cleared in xylol and mounted in Canada balsam.

III. MORPHOLOGY

1. GENERAL CHARACTERISTICS OF THE SPOROPHORES

Schizophyllum is distinctly a xerophyte. The sporophores are found in either of two conditions:

1. In dry weather the sporophores are desiccated, hard, and somewhat brittle (fig. 1, pl. 51). The margin of the pileus is curved inward, decreasing the width of the sporophore about 25 per cent. Each hymenial plate is incurved on the side toward the hymenium. The hymenial surface is hidden and protected. Only the villous sterile surface of the hymenial plates can be seen from the lower side. There is no discharge of spores. This is an inactive period.

2. In moist weather the sporophores take up water and become flexible and leathery in consistency. The pileus margin is only slightly curved downward. The gill plates unroll and extend vertically downward, or nearly so (fig. 2, pl. 51). Spore discharge begins about an

hour after the sporophores are moistened, and continues for a maximum period of about two weeks. However, under natural conditions the period is usually shorter, as the spores cease to fall as soon as the sporophores become dry. Growth takes place, the most actively growing region being at the pileus margin and at the edge of each gill plate. Specimens are naturally most commonly collected when in a dry condition.

The form of the fruit bodies varies greatly, depending in great part upon the position of the surface of the substratum. Thus the sporophores growing upon the under surface of a piece of wood are quite different in form from those found upon the upper surface, and those growing from a vertical surface differ from both of the preceding; but for every one of these three positions the form is fairly constant.

The diversity of form is due to the peculiar organization of the sporophore, the stipe being attached to the upper surface of the pileus, with the hymenophore upon the opposite side of the pileus away from the stipe. Thus *Schizophyllum* differs from all other stipitate members of the Agaricaceae so far studied. This difference was conclusively demonstrated by Hasselbring (1907), who grew the sporophores upon a klinostat. He showed that, when not influenced by the force of gravity, the stipe was always attached near the center of the pileus, but on the opposite side from the "gills." This unusual organization, according to De Bary (1887), is also possessed by *Cyphella*, a member of the Thellephoraceae.

The form which Hasselbring found is the one assumed by fruit bodies growing in nature from the under surface of the substratum. There is a stipe, which is usually short, attached to the center of the upper surface of the pileus. The sporophore is shaped like a broad funnel or bell, the hymenium lining the inner, and also the lower, surface (fig. 1, pl. 52). On a vertical surface the form of the sporophores depends in great part upon the length of the stipe (fig. 2, pl. 52). If this structure is short, it is attached to the pileus near the edge, and the sporophore is ear-shaped. If the stipe is long, it may be curved downward at the outer end and be attached to the pileus near the center, as in specimens grown upon an under surface. Then the shape is that of a curved trumpet. In the ear-shaped forms the stipe is so short that it cannot curve downward, so that the upper edge of the young sporophore is stimulated by gravity (as shown by Hasselbring) to grow more rapidly than the lower edge. Thus the hymenium is

brought into a more advantageous position for spore discharge. On an upper surface the stipe is attached to the pileus at the very edge (fig. 3, pl. 52). The lower edge of the young trumpet-shaped sporophore never develops. The gill plates radiate outward from a place near the attachment of the stipe.

The sporophores are borne singly or in groups. The groups may contain from a few to several scores of specimens attached to each other at the base of the stipe. Sometimes more than one sporophore grows upon a single stipe, but such an occurrence is rare. Only certain members of a group reach maturity, a large percentage never developing beyond a very early stage.

2. DESCRIPTION OF THE MATURE SPOROPHORE

The shape of the individual sporophore varies from broadly bell-shaped with a centrally attached stipe to ear- or racket-shaped with the stipe attached to the edge of the pileus. The edge of the pileus may be entire or more or less deeply lobed. If the lobes are large and deep, they may have secondary lobing. The size of the mature sporophores ranges from 2 mm. to 5 cm. in length and from 3 mm. to 6 cm. in width.

The color of the pileus may be silvery or velvety white, gray, or cream colored. The sterile surfaces of the hymenial plates are a dark gray with often a purplish tint. The hymenium is a shiny brownish-gray. There is a considerable variation in the color of all parts of the fruit bodies, depending upon the age and whether they are wet or dry.

A stipe is usually, but not always, present. Its presence and length depend upon the amount of moisture in the substratum and atmosphere at the early stages of growth, a maximum amount of moisture inducing a greater growth in length. The length varies from 1 mm. to 2 or 3 cm. The form is cylindrical. The stipe rarely attains a width of more than half a centimeter.

The pileus is covered with a dense mass of thick-walled hyphae. If these hyphae are vertical and remain free from each other, the surface appears velvety. If they are agglutinated into groups at the upper ends, the surface is rough and scurfy. If the upper ends form a horizontal layer, the surface has a silvery sheen. The depth of the hyphal covering varies from 1.5 to 2.5 mm. The pileus is made up of thick-walled, septate hyphae. These are closely packed together,

but do not in any case constitute a pseudoparenchymatous tissue. The upper layer of the pileus flesh is pigmented brown.

The lamellar plates extend downward from the pileus (fig. 22, pl. 52). They are arranged in pairs; each pair, with the sterile, hairy surfaces together, giving the appearance of a lamella. Each plate, however, is independent of the other to a certain degree, and may vary from it in size and shape. A hymenial plate may attain a depth of 3 mm., the depth depending entirely upon the number aud length of the growing periods following the origin of the plate, for growth is continuous throughout the duration of favorable conditions. Each plate exhibits a growth region at the margin, which, after the earliest stages, is continuous with and similar to the margin of the pileus. Since the plates arise successively in pairs, a great many different ages and sizes may be found in the same mature sporophore.

The hymenium either covers a much divided single area or is separated into several different areas in the same sporophore, as in plate 53. The elements in the hymenial layer are closely crowded together, and in old specimens tightly adhere to each other, so that a large area of the hymenium may be removed from the subhymenial layer without separating the basidia from one another.

3. MICROSCOPIC STRUCTURE

The study of the microscopic structure of *Schizophyllum* presents considerable difficulty. Upon dehydration the sporophores become hard and brittle, so that the paraffin method of obtaining sections is impracticable. When, by using other methods, sections are obtained, it is found that the hyphal walls are thick, the segments extremely long, and that the nuclei are small and difficult to differentiate by staining.

The vegetative hyphae commonly branch, but not with great frequency. The branching rarely occurs at or near a septum, but usually takes place about the middle of a segment (fig. 1, pl. 54). The hyphae are of two sizes, one having a diameter of 3 to 5μ, and the other being only about 1 or 2μ wide. The finer hyphae are particularly abundant when the mycelium is grown upon artificial media, but are also found to some extent in wood. The hyphae are often covered with small tubercles, as was described by Brefeld (1889) in *S. lobatum* and Miss Rumbold (1910) in *S. commune*. This seems to be a distinctive character. The function of these lateral projections (fig. 2, pl. 54) is not

apparent from their structure. It is possible that they aid in the absorption of food materials, since they closely resemble haustoria in shape and are found only on those hyphae which are purely vegetative. Clamp connections (fig. 1, pl. 54) are found at more than half of the septa in actively growing mycelium. They have been observed upon the hyphae of members of the Hymenomycetes since the earliest studies of their cell structure. Though they occur in a great number of fungi in this group, their exact function is not understood. Harper (1902) suggested that they possibly facilitated the exchange of food materials between segments, but just how this is accomplished is not clear. The length of the segments varies from about 30μ to more than 200μ, the usual length being about 80μ. The thickness of the wall varies from about 0.1 to 0.5μ. In rapidly growing hyphae there are few vacuoles and these are small. The protoplasm is of fine granular structure and very homogeneous. As the mycelium becomes older the vacuoles enlarge, oil droplets are formed, and many of the cells collapse. There are two nuclei to a segment (fig. 1, pl. 54). They are small and spherical, about 0.3 to 0.5μ in diameter. Their structure is granular. No nucleoli have been seen. The nuclei are usually found about 10 to 20μ apart near the center of a segment. These compare very well with the nuclei in the vegetative hyphae of *Hypochnus subtilis* (Harper, 1902, fig. 1, pl. 1). Maire (1900) found but one nucleus in the "cells" of the mycelium of *Coprinus radiatus*.

The hyphae which compose a sporophore are of several different types. One kind includes those which form the hairy covering of the pileus and sterile surface of the hymenial plates; another makes up the pileus and tramal structure, and the third forms the subhymenial layer. Again, each of these types varies somewhat according to the age and state of development of the sporophore.

The hyphae which cover the pileus and sterile surfaces of the hymenial plates are composed in nearly all cases of but a single segment, which may be as long as 3 mm. These hyphae are of a fairly uniform size and length (fig. 3, pl. 54). They are irregularly curved and tangled together. The walls are in the younger stages fairly thin, but as development proceeds they gradually thicken until in very old specimens the lumen has almost entirely disappeared. Two nuclei are present in each hypha of the hairy covering. They are similar in size and shape to those of the vegetative hyphae. They are found regularly near the base of the segment.

The filaments which constitute the solid portion of the sporophore are in their younger stages similar to the larger hyphae which make up the vegetative mycelium (fig. 4, pl. 54). As the fruit bodies become older the segments lengthen, and the walls thicken until they are about equal in thickness to the width of the lumen (fig. 5, pl. 53). When the microscope is focused up and down upon thick sections cut transversely across the hyphae it is seen that the filaments are loosely coiled in a fairly regular spiral, some turning clockwise and others counter-clockwise. In old sporophores the hyphae adhere tightly to each other wherever they are in contact. In the earlier thin-walled state the segments are filled with cytoplasm and have two typical, small nuclei. This is precisely the situation found by Harper (1902) in *Coprinus ephemerus* and *Hypochnus subtilis*. Clamp connections are numerous, but no spine-like tubercles appear. The protoplasmic contents of the thick-walled hyphae of older sporophores are masked by the walls to such a degree that the number of nuclei present cannot be determined. In *Coprinus ephemerus* (Harper, 1902) there are many nuclei in the old "cells" of the pileus and stipe. Maire (1900) found the same to be true in a large number of the fleshy Agaricaceae which he had examined.

The subhymenial layer is composed of hyphae which are thin-walled, and which retain the characters displayed by all the hyphae in their earlier state. Branching is common, and clamp connections are plentiful. There are two nuclei to each segment. The segments are rich in cytoplasm.

The basidia are borne at the ends of thin-walled hyphae. They are only slightly larger in diameter than the hyphae which bear them. All the elements in the hymenium are similar (fig. 6, pl. 54), that is there is no distinction between potential basidia and paraphyses. Mature basidia project beyond the hymenial surface. The basidia come to maturity in succession, only a few in a relatively large area being found with spores attached at any one time. The basidia measure 5 by 20μ. Each has four long, slender sterigmata and bears four spores. Immature basidia display two nuclei. No fusion of these nuclei has been observed, but in later stages four have been seen. It is therefore presumed that the usual fusion and two successive divisions, as described by Wager (1893), Maire (1900), and Harper (1902), have taken place.

The spores *en masse* are white. When seen with the microscope they are nearly hyaline and of an olive green shade. There is a con-

siderable difference of opinion in the literature as regards the shape and size of the spores. The early writers, such as Fries (1821), Cooke (1871), and Saccardo (1887), stated that they were subglobose, about 2.5μ in diameter. Morgan (1890) called attention to the fact that the spores he had been examining averaged 5–6 by 2.5μ, and wondered if a mistake had been made, or if his were possibly a different species. The possibility of a different species seems unlikely, for later Hennings (1898) and Rumbold (1910) in Europe and Murrill (1915) in America have found them to be oblong, at least twice as long as broad. It is possible that the globular bodies supposed by the early writers to be spores were nothing but the peculiar structures which are shed by the dried sporophores when first they are wetted to obtain a spore print. These bodies and no spores are dropped by old herbarium specimens, which have lost their vitality, when they are moistened. The spores occasionally possess small vacuoles. No oil droplets have been demonstrated. The wall is thin. The spores are densely filled with protoplasm. At shedding time two nuclei are present (fig. 7, pl. 54).

The number of nuclei in the spores of the Hymenomycetes so far examined is either one or two. One was found in the spore of *Hypochnus subtilis* (Harper, 1902), *Amanita vaginata, Tricholoma virgatum,* and *Cantharellus infundibuliformis* (Rosenvinge, 1886), while two were found in *Craterellus cornucopioides, Clavaria vermicularis, Boletus edulis,* and *B. variegatus* (Rosenvinge, 1886). Maire (1900), after studying some thirty species, stated that there might be either one or two nuclei in a spore. In the case of two nuclei, the single nucleus divides as soon as it enters the spore from the basidium, instead of just preceding the first segmentation during spore germination.

Spores germinate readily in water and in a great variety of culture media. The spores first swell to nearly twice the normal size; then a germ tube appears at either one or both ends (fig. 8, pl. 54). The width of the germ tube often approximates that of the spore, and as a result the identity of the spore may soon be lost. The length that the tube attains prior to segmentation depends to a certain extent upon the nature of the culture medium, segmentation occurring earlier when the medium is rich in food materials. In tap water growth ceases about the time the first septum and branch appear. Branching may occur either before or after the first septum is laid down, but it usually occurs about that time.

IV. GROWTH OF THE SPOROPHORE

1. DEVELOPMENT IN GENERAL

The development of the sporophores was early looked to for an explanation of the peculiar pairs of hymenial plates which characterize *Schizophyllum*. Fries (1821) believed that they arose as ordinary gills and were split by drying. This view was again brought forward by Fayod (1889), and still later by Buller (1909). Hoffman (1860) believed the sporophore to be divided into a series of lamellar systems, considering all the secondary gills to belong to the primary hymenial plates which enclosed them. His view was adopted by Winter (1884).

Adams recently (1918) made the statement that each lamella consists "of the adjacent walls of two gill cavities which originate endogenously as tubes in the substance of the carpophore. The gill cavities (tubes) split along their lower edges and lamellae are thus completed."

In Hasselbring's (1907) paper on "Gravity as a Form-Stimulus in Fungi" appears the statement that "they [the young sporophores of *S. commune*] appear as small outgrowths resembling simple forms of *Clavaria,* and attain a length of about one centimeter. Early in their development a cup-like depression appears at the summit, and within this the rudimentary lamellae are formed, radiating from the center."

Two distinctly opposed views have, then, been advanced by Hasselbring and Adams. Adams held that the "gills" originated endogenously as the sides of horizontal tubes which later ruptured at the lower edge and exposed the hymenium, while Hasselbring claimed that the "gills" arose exogenously upon the surface of an apical cup-like depression. It seems unlikely that Buller and the previous writers had access to sporophores in the first stages of development, for they made no statements concerning the early appearance of the fruit bodies. Both Adams and Hasselbring, however, grew the sporophores through all their stages in the laboratory. Adams grew his in flasks on agar media from "immature carpophores collected in the field." Hasselbring caused them to grow from "pieces of a maple branch containing the mycelium—placed on a klinostat."

The writer has had an opportunity to study the origin and development of the sporophores both on a log of *Umbellularia californica*

(California Bay) in the field near the laboratory where more than a hundred sporophores have grown during the autumn and winter of 1919–1920; and in the laboratory where scores of sporophores have appeared upon the wood of *Acacia, Quercus,* and *Umbellularia* in moist chambers. Dozens of the fruit bodies have been sectioned, either longitudinally or transversely.

No phenomena in the course of the development of the sporophores have been observed that in any way approximated those described by Adams (1918) for *Schizophyllum commune.* By cutting oblique sections through small mature specimens his figures 2 to 7 in plate 9 may be imitated with fair accuracy, but these sections cannot permit of such an interpretation as he has given for his sections. The crenatures which he shows in figures 2 to 5, plate 9, are entirely absent in all of the 160 or more young specimens the writer has examined. The sporophores which grew here in the laboratory and in the field developed much as was described by Hasselbring (1907).

The fruit bodies appear first as small, loose tufts on the substratum. These develop into small white woolly projections either short and hemispherical or prolonged into horn-like structures, ''resembling simple forms of Clavaria'' (fig. 2, pl. 56). The end is either rounded or conical. These small bodies are covered with loose tangled hyphae. Later the apex becomes smooth, slightly darker in color, and covered with shorter hyphae.

Next a single pore appears at the apex (fig. 3, pl. 56), as Hasselbring (1907) found. Early stages which show the origin of this pore have been difficult to distinguish, as it develops within a few hours after the formation of the buttons or horns, and the loose hairs at the apex screen its first appearance. Longitudinal sections at this stage show first a differentiation of the hyphae just behind the apex (fig. 1, pl. 59). This region stains more deeply than the remainder of the section. The growth at this place is accelerated, and, as increase in size takes place behind the apex, the hyphae at the tip are pulled apart (fig. 2, pl. 59). The hyphae beneath the rupture form a palisade layer which extends laterally into a plane surface (fig. 3, pl. 59). The growth then becomes more rapid at the edge of the layer, producing it outward into a saucer-shaped and later a cup-shaped depression. In this stage it resembles a small sporophore of a *Peziza* (fig. 4, pl. 59).

In all cases observed by the writer the so-called lamellae have originated upon the surface of this apical cavity (figs. 4–14, pl. 52),

which surface constitutes the hymenium primordium. This is exactly as described by Hasselbring (1907), but he did not go into detail concerning the placement or development of the hymenial plates. The pore attains a width of from 1.5 to 2 mm. before the appearance of the first pair of plates. Dozens of specimens in the ''apical depression'' or ''peziza'' stage have been observed where there was no indication of lamellae. By splitting the specimen in half longitudinally the entire surface of the hymenium primordium may be examined with a hand lens. Microscopical examination of prepared sections fails to disclose any indication of closed chambers or of ''gills'' before the ''lamellae'' are plainly visible upon the surface of the hymenium primordium.

The placement of the ''gills'' may be easily observed in actively growing moist specimens (figs. 4–14, pl. 52). They arise as short, isolated ridges upon the surface of the hymenium primordium. The primary ridges arise successively from a point beneath the attachment of the stipe, and grow outward in a radial direction until they finally unite with the edge of the pileus. The secondary ''gills'' originate between the gills already developed, but do not extend so near to the stipe as do those already formed. They occupy, as Buller (1909) noted, an isolated, subterminal position within the interlamellar space in which they have been formed. As growth proceeds, however, the distal ends gradually approach the pileus margin and eventually unite with it, as do the primary ridges.

Soon after a ''gill'' unites with the pileus margin, the pileus becomes split in from the edge, though often this is not disclosed upon the dorsal surface because of the hyphal covering. This marginal splitting is doubtless to some extent hygroscopic, as specimens kept moist from the first are split only slightly, while those subjected to alternate wetting and drying are split farther toward the stipe ends of the ''gills,'' dividing the pileus as well as the hymenium into narrow finger-like projections, the crenatures of Buller (1909).

Occasionally there is an unusual placement of certain ''gills.'' Sometimes they arise at an angle to the radial direction. In this case they frequently remain short and isolated. Often there is a considerable sterile area between the two hymenial plates (fig. 1, pl. 60). This is very commonly found at the stipe end of ''gills'' in lateral sporophores. Rarely the first few primary gills formed unite with each other and the pileus margin to divide the hymenium primordium into several separate areas, in which the secondary ''gills'' later are formed (fig. 15, pl. 52).

Upon a superficial examination the "gills" appear to be much branched. This is especially noticeable in dried specimens (fig. 1, pl. 51). The secondary "gills" are not attached to the primary ones, however, but fit in between and beneath them. Branching occurs but rarely, and is the result of the anastomosing of two "gills" in the early stages of development.

2. ORIGIN AND DEVELOPMENT OF THE "GILLS"

The origin and development of the lamellae has been studied in a fairly large number of members of the Agaricaceae. In all of these Atkinson (1916) recognized two general types. In the first, which he called the "*Agaricus*" type, the hyphae form a palisade layer at the roof of a well-developed annular cavity which appears on the under side of the pileus; and from this palisade layer, which is the hymenium primordium, the lamellae grow downward into the cavity. In the second, or "*Amanita*" type, the gills originate as bars radiating out from the stipe to the under surface of the pileus. The origin and development of the "lamellae" in *Schizophyllum commune* is entirely distinct from either of the above types. The gills grow outward from a palisade layer which forms the lining of a single apical depression or cup.

The origin of a "gill" is evidenced in cross-sections in two ways: either a split appears in the palisade layer and the edges grow outward (fig. 6, pl. 56); or a small area of the palisade layer becomes loosened, grows outward a short distance, and then splits in the middle to a point beneath the original primordial layer (fig. 9, pl. 56). In both cases the growth continues in the same manner. The hyphae beneath the edge of the hymenium on each side of the split grow outward rapidly and cause the hymenial edges to turn downward, and by marginal growth a pair of hymenial plates are soon formed (figs. 1–4, pl. 57). Growth continues at the edges of these plates throughout the life of the sporophore, so that in very old fruit bodies some gill plates may be comparatively deep.

Buller (1909), noting the fact that, in cross-sections of the mature specimens, the tramal layer was split to different depths, thought that the "gills" arose entire and were later split due to hygroscopic tensions. This theory had been earlier advanced by Fayod (1889), who claimed that specimens grown under water have entire "gills." In attempting to demonstrate Fayod's statement it was found that sporophores grow with difficulty under water and decay after a few days.

Those "gills" which did arise under these conditions, however, showed no departure from the proeess as described by the writer above. In all cases observed the plates have been separated at the edges from the very first. In later stages they may be separated only a short distance toward the pileus, or they may be split to any depth in the tramal hyphae or pileus, or even completely through the flesh of the pileus. Each "gill," after it unites with the pileus margin, is split more deeply at the outer end, and the depth decreases toward the stipe end, as does likewise the size of the "gill."

The splitting or loosening of the hymenium to permit the origin of the paired hymenial plates is due to the same tensions which cause the "gills" themselves later to be split to different depths. The addition of new elements to the hymenial layer does not keep pace with the growth of the hyphae beneath the hymenium. When the hymenium has attained a certain width the tension upon the closely crowded elements of the hymenial layer is so great that it is either split longitudinally near the center of the area, or the palisade elements are loosened, grow outward a short distanee, and then split. Likewise the gill plates are split apart to different depths due to the tensions set up by these differences in the rate of growth at different regions of the sporophore. The most rapidly growing region is at the margin of the pileus, and, while growth may and actually does take place throughout the sporophore, it decreases in rapidity from the periphery to the plaee of attachment of the stipe. Thus the gill plates are longer at the periphery, but the differenee between the rates of growth of the hymenium and subhymenial and tramal layers is just as pronouneed. As a result the hymenial margins are incurved more at the margin of the pileus and the gill plates are gradually drawn apart.

In some young sporophores the two hymenial margins are separated by a considerable layer of sterile surface which is level with the hymenium (fig. 1, pl. 60). In this case there is not even a resemblanee to gills.

From the evidence at hand it seems that the so-ealled "gills" of *Schizophyllum commune* Fries are such by analogy only, being aetually two adjacent edges of hymenial areas which arise together, but which become eontinuous with and are homologous to the margin of the pileus. They increase the area of the hymenium as do gills, and, when in a moist condition, look much like typical gills; but eaeh plate is independent of the other from the first, increasing in size by marginal growth.

3. TAXONOMIC INTERPRETATION OF THE STRUCTURE AND DEVELOPMENT OF THE SPOROPHORES

It was early observed that while *Schizophyllum* was presumed to possess gills, the structures were unique among the members of the *Agaricaceae*. Consequently considerable difficulty has been experienced among systematists in associating this genus with the other members of the family from which it is so distinct.

Fayod (1889) believed it to be precisely like *Panus*, except that in *Panus* the gills were entire. He classified them under the tribe Panoides, and noted a similarity in the geographical distribution of the two genera. Hennings (1898), following Saccardo (1887–1895), placed *Schizophyllum* in the tribe Schizophylleae with *Rhacophyllus, Oudemansiella,* and *Pterophyllus,* but stated that the other genera do not seem to belong to this group. Murrill (1915) put it in the tribe Agariceae and subtribe Lepiotanae along with *Marasmius, Lepiota,* and other white-spored members of the Agaricaceae.

All these writers have based their classification upon the assumption that the hymenium in *Schizophyllum* is borne upon the surface of lamellae. Since this is not the case—for the hymenophore while quite complex in structure bears a smooth hymenium—the fungus should be placed in the family Thellephoraceae. In this family it resembles *Cyphella* in the organization of the sporophores, for, in this genus, according to De Bary (1887), the hymenium lines the inner and lower surfaces of a funnel-shaped sporophore, the stipe being attached to the opposite side of the pileus from the hymenium (fig. 16, pl. 52). The early stages in the development of *Schizophyllum commune* and *Stereum hirsutum,* likewise, have much in common. In the later stages, however, the hymenium of *Stereum hirsutum* remains entire, and bears no resemblance to the much divided hymenium of *Schizophyllum commune.* Only in the genus *Cladoderris* is there anything comparable to the hymenial plates of *Schizophyllum. Cladoderris* is somewhat similar to *Stereum,* but differs in possessing radiating, branched ribs upon the hymenial surface. Some species of *Cladoderris* have the pileus margin much incised. The representatives of the genus *Cladoderris* are chiefly tropical, and are known to the writer only through descriptions and illustrations. From these it seems that there is only a difference in degree between the splitting of the pileus margin in sporophores of *Cladoderris infundibuliformis* Fries (cf. Hennings, 1898) and the marginal division in fruit bodies of *Schizophyllum commune.*

V. ECONOMIC ASPECTS

1. GEOGRAPHICAL DISTRIBUTION

In a discussion of the economic importanee of *Schizophyllum* it seems well to go into detail coneerning its distribution throughout the world, as any consideration of the amount of damage done must take into account both its distribution and its abundance in any district. Fortunately a great number of statements have been published concerning its eollection in various places. In the table below are given by continents the countries or regions in which *Schizophyllum* has been eollected or reported, the authority, and the date of publication of the article. The table is representative rather than exhaustive, as only one reference to a locality has been ineluded.

TABLE OF GEOGRAPHICAL DISTRIBUTION

Continent	Place	Authority	Date
Eurasia	England	Cheesman, W. N.	1904
	Scotland	Paterson, R. H.	1877
	Sweden	Linnaeus, C.	1753
	Germany	Hennings, P.	1898
	France	Gueguen, F.	1901
	Italy	Archangeli, G.	1887
	Central Asia	Sorokine, N.	1890
	China	Roumeguère, C.	1879
	Ceylon	Berkeley, M. J., and Broome, C. E.	1871
Africa	Tripoli	Baroni, E.	1892
	Abyssinia	Saccardo, P. A.	1891
	Cape of Good Hope	Berkeley, M. J.	1876
	Africa	Hennings, P.	1891
North America	Canada	Dearness, J.	1896
	Eastern United States	Atkinson, G. F.	1901
	Middle Western U. S.	Heald, F. D.	1906
	Oregon	Griffin, F. L.	1911
	California	Smith, R. E., and E. H.	1911
	Mexico	Patouillard, N.	1887
	West Indies	Massee, G.	1892
South America	Brazil	Averna-Sacca, R.	1916
Australia	Australia	MacAlpine, D.	1902
	New Zealand	Buchanan, J.	1874

The sporophores of the *Schizophyllum* in the field are usually small and inconspicuous. When found they are usually in large numbers within a small area on a log or tree. Only an oecasional tree or log displays them in this region (California). Heald (1906) reported that every tree of a small orchard of cherries in Nebraska was infected with the fungus, but this seems to be an extreme case.

2. LIST OF HOST PLANTS

A large number of plants have been mentioned in scientific literature as hosts of the sporophores of *Schizophyllum*. It is not clear in most of these references whether the specimens were found upon living or dead plants. The distinction is of some importance in the consideration of the economic aspects of the fungus. The information in the following table has been obtained from publications, from the spoken word of collectors whom the writer has been fortunate enough to meet, from specimens in the Herbarium of the University of California, and from observations in the field. Dates are given for references to publications only.

TABLE OF HOST PLANTS

Family	Name	Authority	Date
Pinaceae	Yellow Pine (*Pinus ponderosa*)	Stillinger, C. R.	
	Western Hemlock (*Tsuga heterophylla*)	Stillinger, C. R.	
Gramineae	Sugar Cane (*Saccharum officinarum*)	Ray, J.	1896
	Bamboo (*Bambusa* sp.)	Horne, W. T.	
Palmaceae	Royal Palm (*Oreodoxa regia*)	Horne, W. T.	
Juglandaceae	English Walnut (*Juglans* sp.)	Smith, R. E., and E. H.	1911
	Hickory (*Hicoria* sp.)	Dearness, J.	1896
Betulaceae	Alder (*Alnus* sp.)	Linnaeus, C.	1783
	Birch (*Betula* sp.)	Adams, J. F.	1918
Fagaceae	Beech (*Fagus* sp.)	Rumbold, C.	1910
	Oak (*Quercus serrata*)	Roumeguère, C.	1879
	Chestnut (*Castanea* sp.)	Stevens, F. L.	1913
Moraceae	Mulberry (*Morus* sp.)	Prillieux and Delacroix	1893
Lauraceae	California Baytree (*Umbellularia californica*)	Brown, V. S.	
Rutaceae	Oranges and Lemons (*Citrus* sp.)	Smith, R. E., and E. H.	1911
Tiliaceae	Linden (*Tilia* sp.)	Hennings, P.	1898
Aceraceae	Maple (*Acer* sp.)	Hasselbring, H.	1907
Hippocastanaceae	Horse Chestnut (*Aesculus Hippocastanum*)	Gueguen, F.	1901
Rosaceae	Apple (*Pyrus malus*)	Fulton, H. R.	1912
	Pear (*Pyrus communis*)	Baroni, E.	1892
	Cherry (*Prunus cerasus*)	Griffin, F. L.	1911
	Peach (*Prunus persica*)	Camp, A. F.	
	Almond (*Prunus communis*)	Kellogg, E. S.	
Leguminosae	*Pterocarpus indicus*	Kew Bull. Misc. Inf.	1910
	Acacia (*Acacia* sp.)	Seen in the field	
	Hardy Catalpa (*Catalpa speciosa*)	Stevens, N. E.	1912
Rubiaceae	Coffee (*Coffea* sp.)	Averna-Sacca, R.	1916

3. EXTREME HARDINESS OF THE FUNGUS

Schizophyllum is able to persist under very adverse circumstances. Its unusual vitality is displayed in three ways: (1) the sporophores are able to endure long periods of drought; (2) the mycelium can grow upon almost any moist organic substance; and (3) the sporophores possess the ability to regenerate lost parts.

Buller in 1909 called attention to the long period over which the sporophores can retain their vitality. He stated that "whilst in the dried condition a fruit body can retain its vitality for at least two years, and, with intermittent revivals, for at least three years." Later (1912) he and Cameron found that the fruit bodies could endure sudden changes of temperature, suspension in a vacuum, extreme cold, or a long period in darkness. In this respect they resemble certain seeds and mold spores.

A mycelium produced either from spores or pieces of sporophores will grow upon a whole series of substances. Some of the materials upon which the hyphae grow well are such starchy media as potato tubers, corn meal, rice, "Cream of Wheat," and lima beans; sugary media such as beets, prune juice, and grapes; upon agar and gelatin nutritive media; and upon dung, a wood decoction, or dead leaves. Kellogg (1915) grew the fungus from spore to spore, or through all of its life history, upon sterilized potato plugs in glass flasks, showing that *Schizophyllum* can exist in an entirely saprophytic condition. Earlier Rumbold (1910) had produced sporophores on bread from spore cultures, but, although these bore basidia on a definite hymenium, no spores developed.

Experiments have been carried on to determine to what extent the sporophores can regenerate lost parts. The fruit bodies studied were grown upon blocks of *Acacia* wood kept in moist chambers in the laboratory. In one case about one-half of the pileus at the distal ends of mature sporophores was removed by cutting with a sharp knife. Some of the specimens were left in the original position, and others were inverted by reversing the position of the blocks of wood upon which they were growing. Where the mutilated sporophores were left in position growth ceased at the cut edge, but continued in a normal manner, though rather slowly, at the pileus margins to the side. Most of the inverted specimens ceased growth altogether. In one case, however, in a few days the margin at one side began to turn and grow outward in a horizontal direction with the hymenium facing

downward. At the end of 17 days a normal sporophore about 1 cm. in diameter had developed (fig. 2, pl. 60).

In another experiment the entire hymenophore was removed by cutting across the stipe at the distal end. Specimens left in the original position produced new hymenophores in one of two methods. If the stipe was small at the cut end, only one new sporophore, as a rule, developed by the growth of hyphae out through the cut end of the stipe (fig. 3, pl. 60). This developed in the usual way. If the cut end of the stipe was of considerable area, several small sporophores developed. These grew in the usual way except that the hymenial plates arose in position with respect to the old stipe and not as though the separate sporophores were distinct individuals (fig. 18*d*, pl. 52). The sporophores more advantageously placed, that is, at the upper edge of the stipe, grew more rapidly and became much larger than those at the sides. The sporophores might be cut away to within a millimeter of the base of the stipe and still a new sporophore would develop upon the cut end. The specimens used were mature and were shedding spores, but were comparatively young. Thus the sporophores have, at least while still young and fresh, the ability to regenerate practically the entire body.

Stipes with the entire hymenophore removed and in an inverted position in all cases produced either one or several small sporophores upon the cut end, but growth soon ceased. Sections through these specimens showed that they had stopped growing either in the "peziza" stage or after one or two hymenial plates had been formed (figs. 19–20, pl. 52). The inability of the sporophores to develop further in an inverted position is doubtless due to their lack of power to change the polarity of the different parts with respect to the reaction to the force of gravity. That gravity is the form-stimulus was clearly demonstrated by Hasselbring (1907).

4. RELATION OF THE MYCELIUM TO CELLS OF DEAD WOOD

Upon sectioning dead wood it is found that there is an unexpected paucity of mycelium in the tissues infected by *Schizophyllum*. Wood brought in from the field in a dry condition covered with the sporophores may be sectioned and fail to display any mycelium in a large percentage of the sections. In some, however, a few hyphae can be seen.

The hyphae of this fungus are shown by sections to be confined almost entirely to the tracheae of the wood (pl. 61). In some ducts

there may be only one or two, but in others the lumen may be almost filled. In all cases the mycelium varies considerably in size, the walls are thin, and branching is infrequent. The lateral tubercles are present upon the walls of some of the hyphae.

Wherever the mycelium is found in wood in earlier stages of decay there is present a series of small, globular masses of a brown exudate. The mycelium of *Schizophyllum* growing upon artificial media produces a like substance, so that found in the wood is probably produced by the hyphae. In certain regions the droplets are so numerous that the wood is discolored. They account for the black or dark brown layers often seen near the edge of the decayed areas. In regions of advanced decay they have entirely disappeared.

Cross-sections through the limb of a living tree which was infested with the fungus in a narrow area along one side of the limb showed that the infected area extended in a radial direction to the center of the limb. Some pieces of this limb were placed in moist chambers. In a few days tufts of hyphae grew out of the wood at the edges of the infected area near the living wood and only a few scattering threads could be seen in the central part of the discolored tissues. Thin sections also disclose the fact that the greater part of the vegetative mycelium is near the living wood in partially killed limbs or trunks of trees.

The decay is marked at first by a darkening of the tissues. There are dark brown or black layers near the edge of the darkened areas. At later stages delignification sets in, and the decayed areas become straw-colored. The cell walls become softened, but retain their structure for a long period. The mycelium of *Schizophyllum* is frequently found in areas of advanced decay along with the hyphae of other fungi, and it is difficult to determine how much of the decay is due to the work of *Schizophyllum commune* alone.

5. GROWTH UPON FRESH WOOD AND LIVING TISSUES

Freshly cut pieces of Acacia wood were placed in moist chambers and spores of *Schizophyllum* were planted upon different tissues. Acacia wood was chosen because sporophores are found in abundance upon the dead wood of this tree. The pieces of wood were kept moist enough to cause the spores to germinate. The experiment was carried on for two months. At the end of that time it was found that the

hyphae had not penetrated through the fresh, uninjured bark, or cortical tissues, or through the wood tissues in a lateral direction, but had grown through the wood in the direction of the tracheae.

Attempts to prove the parasitism of this organism were made by Gueguen (1901) and Fulton (1912) with negative results. Rumbold (1910) stated that Tuzson (1905), (whose paper is not available) grew the fungus upon fresh (*frais*) beech wood. Kellogg (1915) was not able to demonstrate the mycelium of *Schizophyllum* in the inoculations made upon fruit trees.

In my inoculation experiments young fruit trees of apple, pear, and plum were used. Inoculations were made from agar plates of pure cultures of the mycelium. The limbs of these trees were either split through the center or cut into from the surface to varying depths. A sterile knife was used in the incisions. The mycelium with substratum was transferred to the cut or slit surface and the wound was tied up with string and covered with waxed paper, a layer of wet absorbent cotton, and another layer of waxed paper. The purpose of the wet cotton and waxed paper was to prevent the drying out of the exposed surfaces. At intervals of one week after the time of inoculation certain limbs were removed, examined, and sections made to determine if there had been any growth of the mycelium into the living tissues. In most cases no trace of the mycelium could be found in the wood. In two or three branches there was a darkening of the surface exposed to the mycelium, and in the vessels the typical exudate which is produced by the mycelium, but so little mycelium was found in the ducts that the growth could not be identified, with certainty, as *Schizophyllum*. In only one branch was there an unmistakable infection. This was in a limb of a plum tree cut off three months after inoculation. The mycelium had penetrated to a maximum depth of 3 mm. and the infected area was about 4 cm. long and 1 cm. in width. Many hyphae were present in the vessels, and a few could be seen in the medullary ray cells. There was the characteristic darkened layer at the edge of the infection about 0.5 mm. thick. From the results of previous investigations and these experiments it is evident that the living woody tissues can be penetrated and killed by the mycelium of *Schizophyllum*, but that this process takes place slowly and with difficulty.

6. METHODS OF INFECTION UNDER NATURAL CONDITIONS

There have been many expressions of opinion in published papers concerning the manner in which living trees become infected with the mycelium of *Schizophyllum.* Infection takes place in three more or less distinct ways: (1) by entering through surfaces exposed by mechanical injury, (2) by attacking parts of trees weakened through certain physiological causes, and (3) by gaining admission through tissues first injured or killed by other organisms.

As regards mechanical injury, in Stevens and Hall (1910) it is stated that "apparently this disease starts in roots injured by tools during cultivation." Professor Horne of the University of California has observed an infection beneath an apple tree graft (fig. 1, pl. 58) that had not been properly sealed with wax. An infection at a crotch split in a peach tree (fig. 2, pl. 58) was reported by A. F. Camp, a student in the University of California. Any woody part exposed by injury forms a possible place of entrance for the fungus.

Weakening of the trees by excess water, or lack of proper drainage, was decided by Guegen (1901) to be a contributory cause of infection in horse chestnut trees. Stone (1910) found that sun scald and scorch of maple trees was followed by *Schizophyllum* and other fungi. The writer has seen the sunburned parts of California Bay trees covered with sporophores. It is evident that trees weakened by certain physiological agents fall prey to this fungus, and probably any loss of vitality on the part of the tree makes it susceptible to the attacks of *Schizophyllum.*

Wilson (1912) found that the sporophores issued through the burrows made by the shot hole borer (*Xyleborus dispar* Fabricus). Griffin (1911) stated that cherry trees weakened by bacterial gummosis are frequently attacked and killed by *Schizophyllum commune.*

No evidence has been brought forward in available literature to show that *Schizophyllum* is able to infect healthy trees, or those not injured or weakened in some way. It seems likely that infection can be prevented by using care in cultivation, by painting wounds made in pruning, by preventing crotch splitting, by protecting the trees from sunburning, and by keeping them free from other diseases.

7. ASSOCIATION WITH OTHER WOOD DECAY FUNGI

Fulton (1912) found that in an apple collar rot which he described *Schizophyllum commune* was present along with two other organisms.

Stone (1910) found in sun scald and scorch of maples that it was followed first by a canker fungus (*Nectria cinnabarina*), and then by *Schizophyllum* and *Polystictus.*

In the case of the apple graft mentioned above, the writer took the branch, sawed it into sections, and placed some of the sections in a moist chamber. From the decayed area a mass of mycelium appeared which was not of *Schizophyllum,* but as it has not yet produced any fruit bodies it cannot be identified.

Observations show that the fruit bodies of *Schizophyllum* are produced in a comparatively short time after inoculation has taken place. I have noted several times in the field that this fungus is the first to appear upon uprooted trees. Later, sporophores of *Polystictus, Polyporus, Tremella, Hydnum,* and other fungi are produced. Most of the pieces of wood I have collected in the field, which have only sporophores of *Schizophyllum* upon them, when placed in moist chambers long enough will produce sporophores of *Hydnum* or *Polystictus,* or both, long after a great number of fresh *Schizophyllum* fruit bodies have been formed. Since the hyphae of these other fungi were in the wood along with that of *Schizophyllum,* it is apparent that the latter fungus develops sporophores in a much shorter time than the others present. *Schizophyllum,* forming fruit bodies first upon a diseased tree, is naturally accused of being the parasite causing the damage. The writer believes that much or even most of the injury to trees attributed to this fungus is actually caused by the fungi so often associated with it, such as *Polystictus versicolor,* which is beyond doubt a parasite.[2]

[2] Proof of the parasitism of *P. versicolor* was given by W. W. Thomas in 1916 at the University of California in a thesis submitted for a Master's degree. Mr. Thomas inoculated living trees with positive results as regards infection.

VI. SUMMARY AND CONCLUSION

In summarizing the morphology and development of *Schizophyllum* it may be said that:

1. The sporophores vary greatly as to form and shape.

2. The segments of the mycelium and sporophores and spores are regularly binucleate.

3. The fungus develops its sporophores as does no other member of the Hymenomycetes so far studied, the hymenium primordium arising in an apical cavity.

4. The ''gills'' arise upon the surface of an apical depression due to tensions set up by unequal rates of growth.

5. The ''lamellae'' are such by analogy only, being the edges of smooth hymenial areas, and therefore *Schizophyllum* belongs in the family Thellephoraceae.

As regards the economic aspects of *Schizophyllum*, it has been shown that:

1. Members of this genus are found throughout the tropical and temperate zones of the world.

2. They live upon a great number of woody plants, both in the Dicotyledonae, Monocotyledonae, and Gymnospermae.

3. The fungus possesses unusual vitality.

4. The mycelium is found only in small amount in infected wood.

5. It can grow upon fresh wood, and, under very favorable conditions, living wood.

6. Natural infection takes place through some injured or weakened part of the tree.

7. The fungus is usually associated with other parasitic fungi, which probably do most of the damage attributed to *Schizophyllum*, but escape attention due to the longer time necessary for them to produce fruit bodies.

VII. ACKNOWLEDGMENTS

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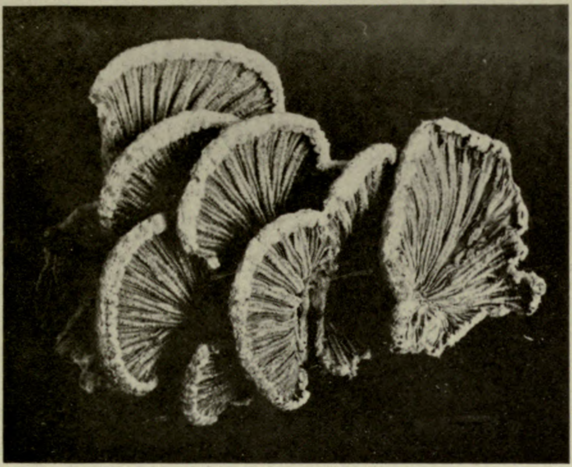
EXPLANATION OF PLATES

PLATE 51

Fig. 1. Group of sporophores in a dry condition, viewed from the lower side. 2 diameters.

Fig. 2. Group of sporophores in a moist condition, as seen from below. Some of the smaller specimens at the base of the group have been cut away. $1\frac{1}{2}$ diameters.



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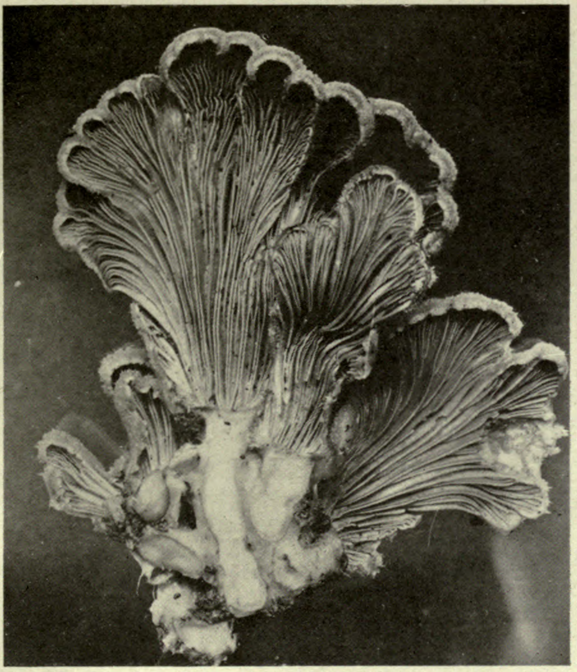

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PLATE 52

Fig. 1. Form of sporophores growing upon an under surface. *a,* side view of fruit bodies in position. *b,* the hymenium of a typical fruit body viewed from below, showing the gill plates radiating outward from a region near the center of the hymenium. ½ natural size.

Fig. 2. Form of fruit bodies growing upon a vertical surface. *a,* three sporophores in position. *b,* arrangement of the lamellar plates in a sporophore grown upon a vertical substratum. ½ natural size.

Fig. 3. Form of fruit bodies growing on an upper surface. *a,* position assumed by sporophores upon the upper surface of a limb. *b,* typical arrangement of the lamellar plates. ½ natural size.

Figs. 4–15. Views of young actively growing fruit bodies from the under side to show the origin and placement of the lamellar plates or ridges. All 5 diameters. Fig. 4, a sporophore with a smooth hymenium primordium just prior to the formation of lamellar ridges. Fig. 5, a fruit body with a single lamellar ridge. Fig. 6, a single lamellar ridge with the sides so far separated by sterile hyphae as to become merely edges of the hymenium primordium. Fig. 7, a specimen with four newly formed lamellar ridges. Figs. 8–14, six sporophores with some isolated ridges and some extending to the edge of the pileus. Fig. 15, a lateral sporophore with the lamellar ridges widening into sterile areas towards the base.

Fig. 16. Sporophore of *Cyphella Urbani.* 3 diameters. (After Engler and Prantl.)

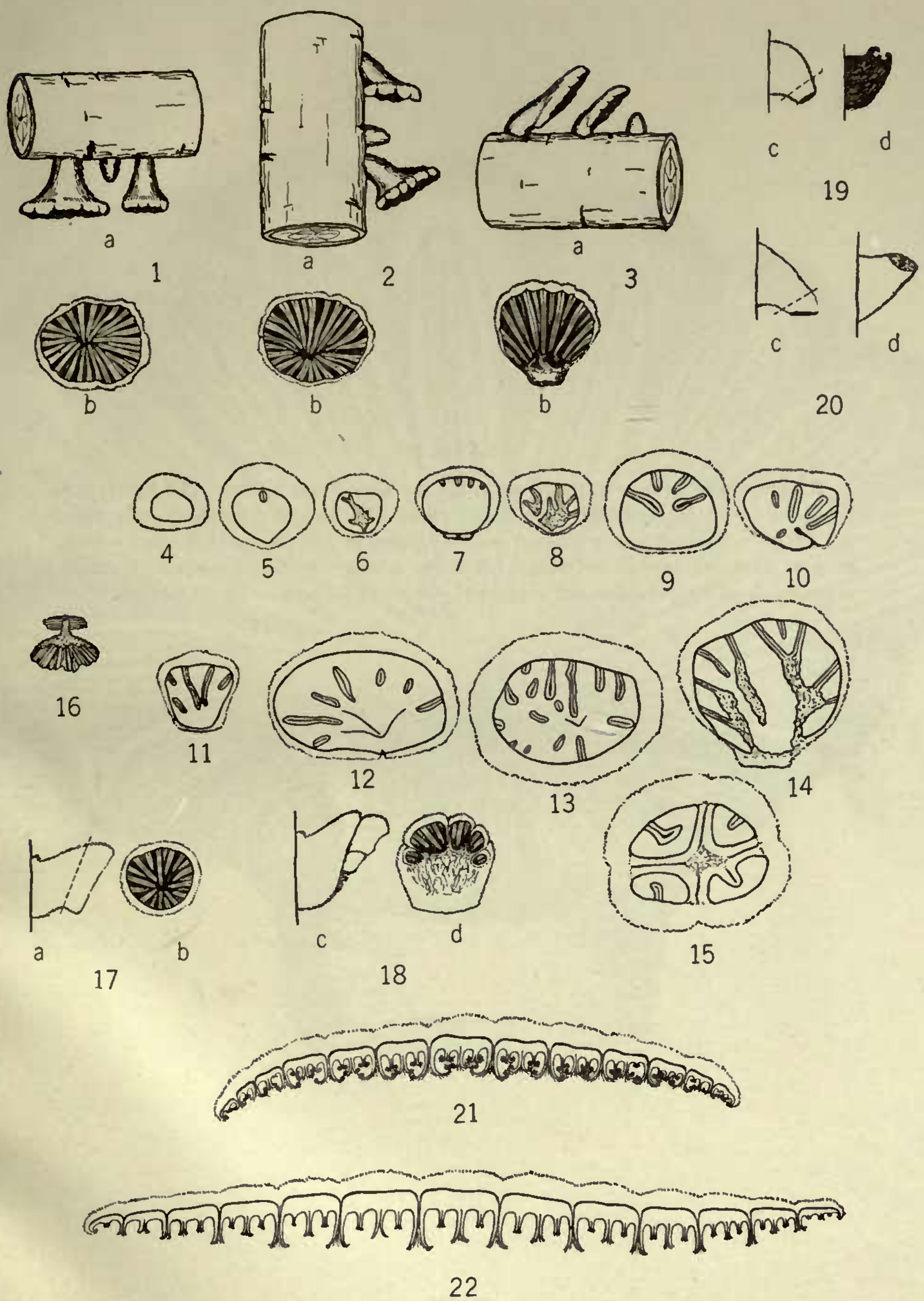
Figs. 17–18. Regeneration in position. *a,* a small sporophore showing with a broken line where the hymenophore was removed. *b,* face view of the hymenophore removed. 18*c,* side view of the sporophore after seven days. *d,* face view of the same, showing five small sporophores formed upon the cut end of the old stipe. All 1½ diameters.

Fig. 19. Regeneration inverted. *c,* a small fruit body showing where the end was cut away. *d,* a median section of the same thirty days later. Only one pair of lamellar plates was formed. 1½ diameters.

Fig. 20. Regeneration inverted. *c,* a small sporophore showing where the end was removed. *d,* the same a week after the apex had been cut away, showing three very small sporophores formed upon the cut end of the inverted stipe. These developed no further. 1½ diameters.

Fig. 21. A transverse section through a sporophore when in a dry state, showing the revolute lamellar plates, and their arrangement. 5 diameters.

Fig. 22. A transverse section through the same sporophore represented in fig. 21, but drawn while the sporophore was in a moist condition. 5 diameters.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a
2
a
3
b
b
b
c
d
19
c
d
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4
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10
16
11
12
13
14
a
b
17
c
d
18
15
21
22

PLATE 53

A sporophore in a semi-moist condition, as seen from below. The hymenium is shown to be divided into four areas, three of which are much smaller than the fourth. Several newly formed isolated pairs of lamellar plates can be seen, as well as three very small ridges near the center of the hymenophore which arose in an early development stage but remained isolated. 10 diameters.

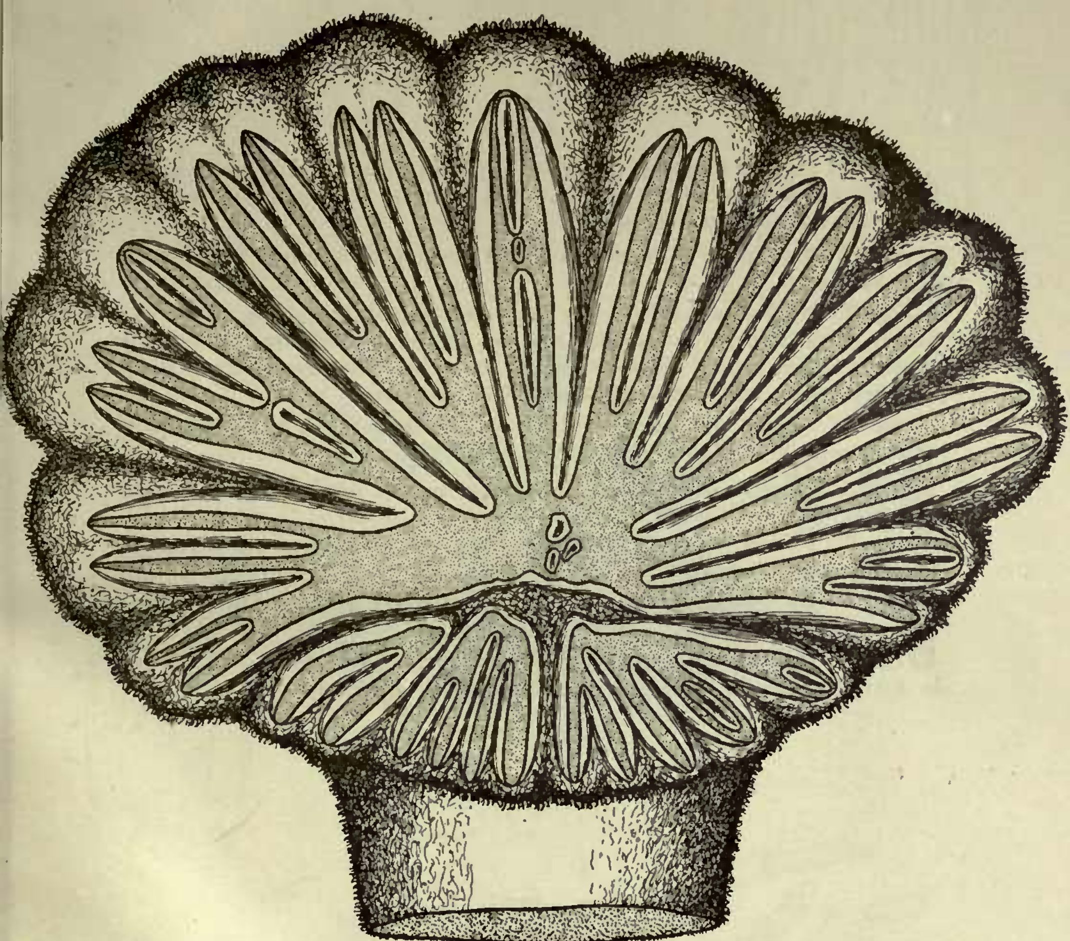

PLATE 54

Fig. 1. Part of a typical vegetative hypha to show the structural characters. Clamp connections are shown at each septum. The nuclei are near the center of each cell. 1500 diameters.

Fig. 2. Portion of a vegetative hypha covered with lateral projections. 1500 diameters.

Fig. 3. Hyphae which form the hairy covering of the pileus. They are usually unicellular, the nuclei being near the base of the cell. In this drawing a portion of each cell 1.4 mm. long was left out. This would represent a distance of about 210 cm. on the drawing paper. 1500 diameters.

Fig. 4. Portion of a longitudinal section through the flesh of a very young sporophore to show the hyphal structure. 1500 diameters.

Fig. 5. Same as in fig. 4, except that the section was taken from an old sporophore. 1500 diameters.

Fig. 6. Portion of the hymenium, showing one mature and one immature basidium. 1500 diameters.

Fig. 7. Six typical spores, stained in safranin and gentian violet to show the nuclei. 2500 diameters.

Fig. 8. Germinating spores in various stages of development after being in distilled water for 48 hours. Stained in safranin. 1500 diameters.

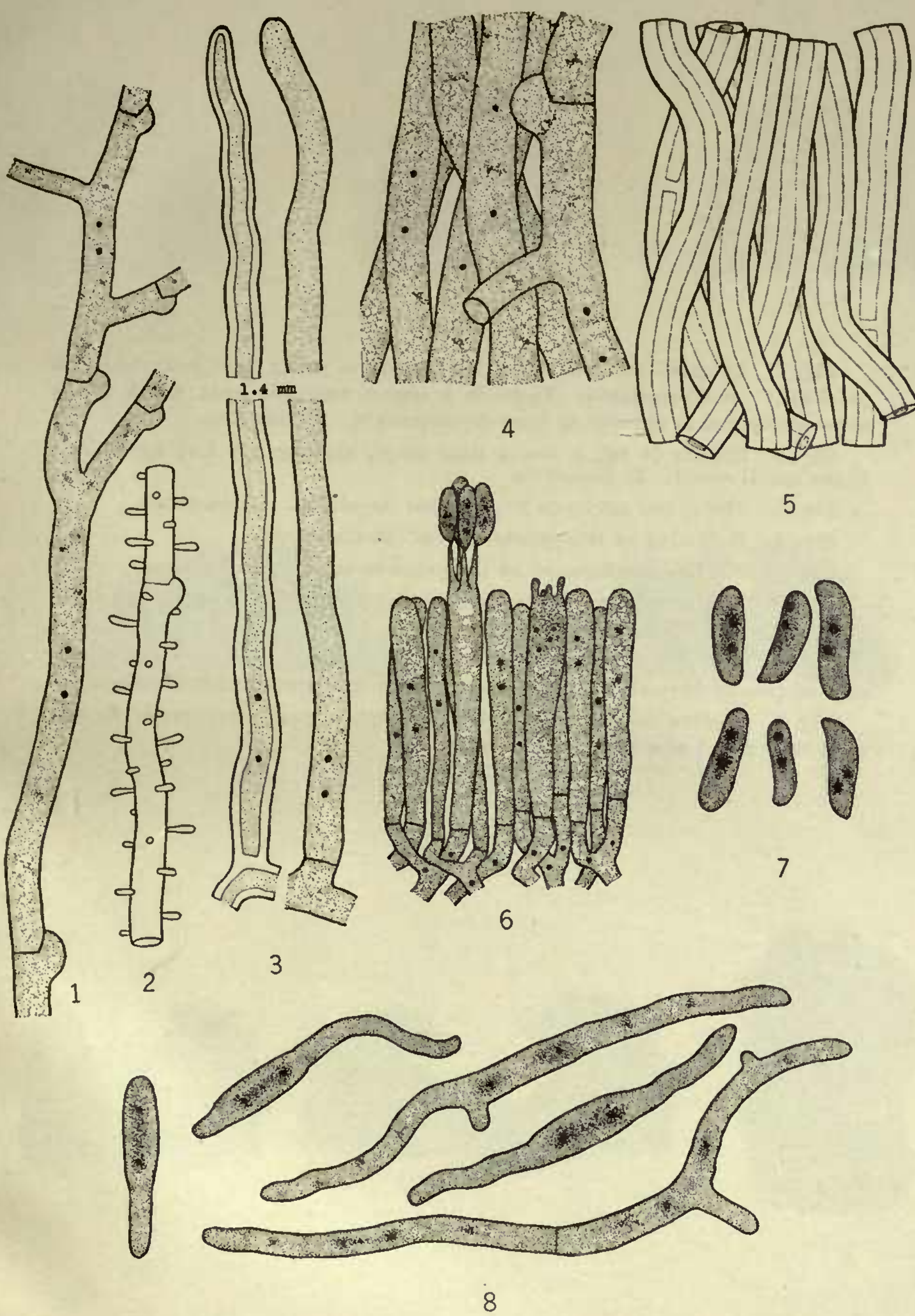
1.4 mm
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PLATE 55

Fig. 1. Longitudinal median section through a young fruit body which is practically undifferentiated. There is a region near the apex which stains more deeply and is the seat of later developments. 25 diameters.

Fig. 2. Similar to fig. 1, but a later stage, showing the first appearance of the apical cavity. 25 diameters.

Fig. 3. The apical cavity is still further developed. 25 diameters.

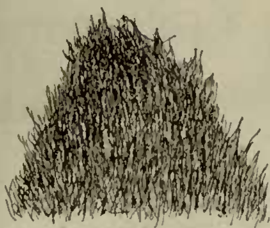
Fig. 4. Beginning of the palisade layer. 25 diameters.

Fig. 5. Further development of the palisade layer. 25 diameters.

Fig. 6. Maximum growth of the palisade layer in a plane surface. 25 diameters.

Fig. 7. The palisade layer (hymenium primordium) produced into a concave surface by the outward growth of the edges of the pileus. 25 diameters.

Fig. 8. Median longitudinal section through a small sporophore formed upon the cut end of a stipe. 18 diameters.



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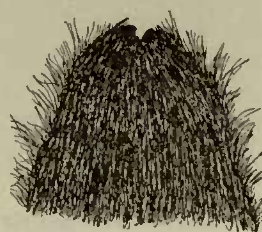

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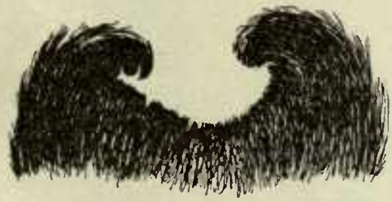

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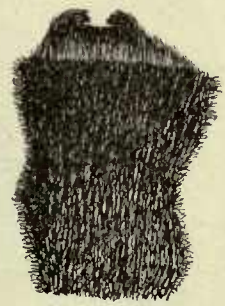

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PLATE 56

Fig. 1. A piece of wood removed from the surface of an *Umbellularia* log, showing a number of very small sporophores in the earliest stage of development. Surface and side views. 2½ diameters.

Fig. 2. Shapes assumed by very young undifferentiated fruit bodies. 2½ diameters.

Fig. 3. A group of young fruit bodies in position upon a piece of *Umbellularia* bark. Five of the specimens are in the ''apical cavity'' stage, one is still undifferentiated, and another (at the extreme right) has already developed lamellar plates. 3½ diameters.

Fig. 4. Tangential section of *Acacia* wood to show the mycelium of *Schizophyllum commune* in a duct. About 125 diameters.

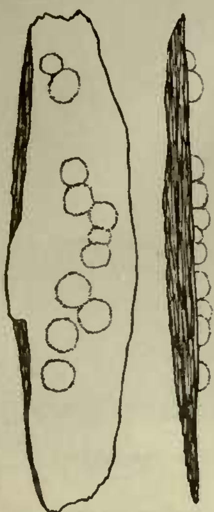
Fig. 5. Radial section of *Umbellularia* wood to show the hyphae of *Schizophyllum* in the ducts. About 125 diameters.

Fig. 6. Splitting of the palisade layer previous to the formation of a lamellar ridge. 250 diameters.

Fig. 7. Outward growth of the palisade layer at the sides of a split. 250 diameters.

Fig. 8. Loosening and outward growth of the elements of the palisade layer to form a lamellar ridge. 250 diameters.

Fig. 9. Cross-section of the palisade layer to show a very early stage in the origin of a lamellar ridge. 250 diameters.



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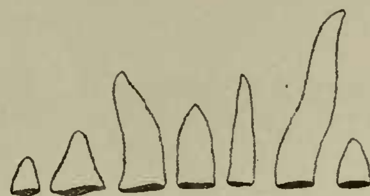

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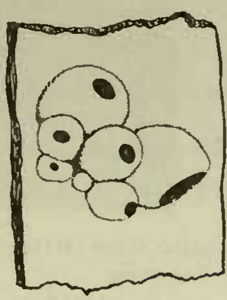

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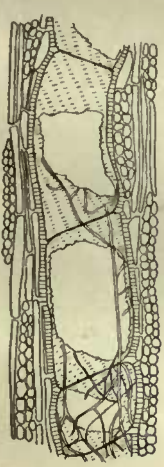

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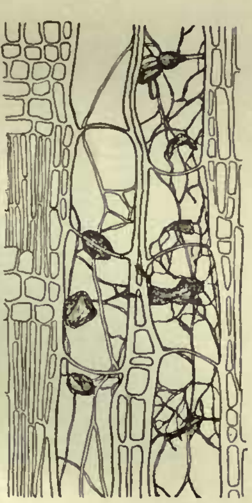

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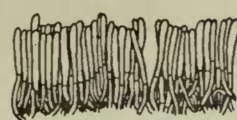

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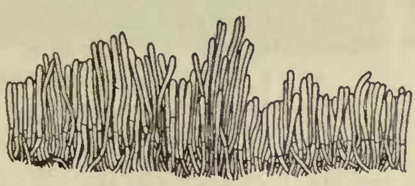

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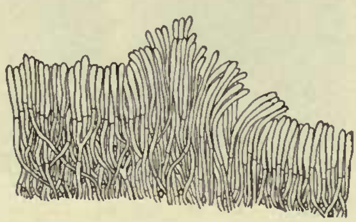

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PLATE 57

Fig. 1. A transverse section across a lamellar ridge in a very early stage of development. 448 diameters.

Fig. 2. A cross-section through a lamellar ridge divided down in the middle to form two small lamellar plates. 448 diameters.

Fig. 3. Another lamellar ridge in a stage of development similar to that shown in fig. 2. 448 diameters.

Fig. 4. A lamellar ridge whose halves are split apart deeply into the pileus flesh. 448 diameters.

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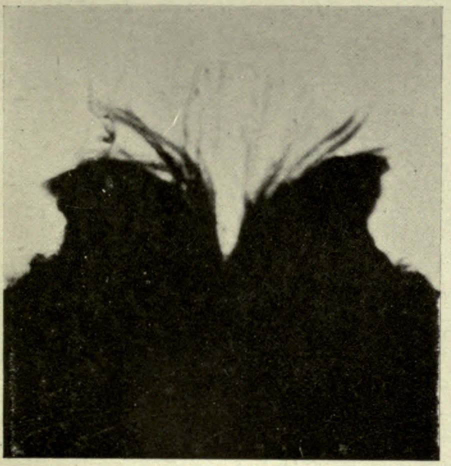

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PLATE 58

Fig. 1. Sections of apple limbs with the wood rotted by fungi penetrating through an improperly sealed graft. Sporophores of *Schizophyllum* appeared upon the bark of the tree beneath the graft about a year after the grafting was done. See the text for further explanation. ½ natural size.

Fig. 2. Sporophores of *Schizophyllum commune* in a dry condition upon the bark of a living peach tree at the side of a crotch split. The lower end of the split can be seen on the right side of the trunk. ½ natural size.

1

2

PLATE 59

Fig. 1. A median longitudinal section through a very small undifferentiated fruit body. See fig. 1, pl. 54. 55 diameters.

Fig. 2. A median longitudinal section of a sporophore showing the breaking in of the apical cavity. 55 diameters.

Fig. 3. Photomicrograph of the section drawn in fig. 6, pl. 54. 55 diameters.

Fig. 4. A median longitudinal section through a fruit body with the apical cavity fully developed. 55 diameters.

1

3

2

4

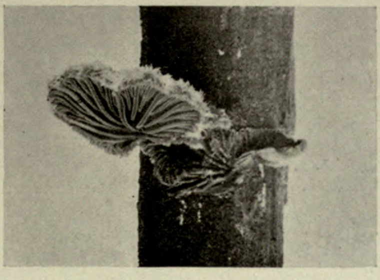
PLATE 60

Fig. 1. A widened lamellar ridge in cross-section, showing the sterile area between the edges of the hymenium. 75 diameters.

Fig. 2. A sporophore developed from a single lobe of a mutilated inverted specimen. For a further description see the text. 2 diameters.

Fig. 3. A median longitudinal section through a regenerated sporophore. See text for further explanation. 75 diameters.

1



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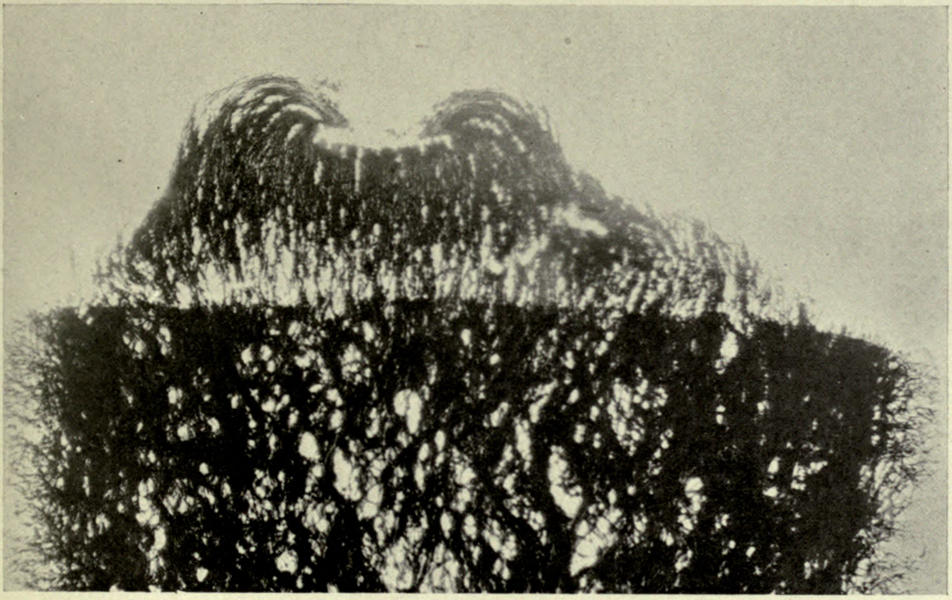

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PLATE 61

A radial section through *Umbellularia* wood with the hyphae of *Schizophyllum commune* in the tracheae. 350 diameters.

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